

## OXYGEN BALANCE IN SOME REEF CORALS<sup>1</sup>

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Ecologists have been intrigued by the seeming paradox of the biological richness of coral reefs in the middle of relatively barren tropical seas. It has been debated whether such a community lives mostly off material in the water passing over it or whether it produces at least part of its required fixed carbon by local photosynthesis (Yonge *et al.*, 1932; Odum and Odum, 1955; Ryther, 1959). The latter thesis is suggested by the large numbers of unicellular algae within the living cells of the coral and the boring filamentous algae in the non-living skeleton of the coral.

Others have shown that under certain experimental conditions, a coral head may produce more oxygen by photosynthesis than it consumes by respiration (Yonge *et al.*, 1932; Kawaguti, 1937; Odum and Odum, 1955; Burkholder and Burkholder, 1960; Beyers, 1963 and 1966; Franzisket, 1964; Roffman, personal communication). We have extended this work by continuously monitoring oxygen tension in the experimental chamber at different light intensities and by relating oxygen tension to the area of the coral head receiving light. The coral heads we used include the coral animals, their intracellular dinoflagellates (zooxanthellae) plus, in stony corals, the filamentous green algae residing inside the non-living  $\text{CaCO}_3$  skeleton, and any number of animal species and micro-organisms that may also inhabit the skeleton. From such measurements we find isolated coral heads to be nearly as productive as any other organisms in nature, yielding values up to 10 grams carbon fixed per square meter of reef per day. In addition our data indicate that most of the photosynthesis is that of the zooxanthellae. Whether this productivity actually nourishes the coral animals will only be determined by tracer experiments and by quantitative observations of corals with and without zooxanthellae.

### MATERIALS

Oxygen balance experiments were carried out on the following species of corals:

Octocorallia, Gorgonacea:

*Plexaura flexuosa* Lamouroux

*Gorgonia ventalina* L.

*Briarum asbestinum* (Pallas)

*Erythropodium caribaeorum* (Duchassaing & Michelotti)

Zoantharia, Scleractinia

*Siderastrea siderca* (Ellis & Solander)

*Porites divaricata* Lesueur

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*Favia fragum* (Esper)  
*Manicina arcolata* (L.)  
*Montastrea annularis* (E. & S.)  
*Oculina diffusa* Lamarck  
*Dichocoenia stokesii* Milne-Edwards & Haime  
*Mussa angulosa* (Pallas)  
*Isophyllia multiflora* Verrill  
*Colpophyllia* sp.

Corals were collected from patch reefs identifiable on U.S. Coast and Geodetic Survey charts of the Florida Keys as "Hen and Chickens" and "The Rocks," both southeast of Plantation Key. Maximum depths at the two sites are 9 m. and 5 m., respectively. Each coral was collected by divers trained to select for size and shape to fit respirometer chambers, for paucity of associated biota, and for ease in collecting and handling. Corals were chipped off the reef with geologists' picks and handled only by their non-living bases so that their tissues were neither touched by hand or tool nor exposed to air in being transferred from reef to laboratory to respirometer. It is important to state that the tissues of stony corals are only four layers of cells thick and that when they are exposed to air or when they are stimulated to contract strongly by being touched in handling, the delicate tissues are perforated in many places by their own  $\text{CaCO}_3$  skeletons. Experiments performed with animals collected without such care are thus dealing with wounded, presumably regenerating animals. The qualitative and quantitative effects of this treatment on the normal functions of any coral species are unknown and it is therefore desirable to avoid this trauma.

Corals were maintained in sea water in a plastic wading pool. Many more specimens were collected than were used experimentally. Criteria for experimental suitability were the expansion of polyps in the lab at the same time of day the species were observed to be expanded on the reef, and sensitivity of expanded polyps to being jarred or touched that seemed, subjectively, to be similar to sensitivities observed of the species on the reef. Epifaunal organisms were carefully picked off each specimen. In every case but one, corals with polyps expanded were put into the respirometer without being caused to contract completely. All handling was done under sea water. Immediately upon assembly of the respirometer, all specimens expanded their polyps.

We have had little confidence in most previous determinations of coral productivity for a variety of reasons. Foremost is the suspicion that goes with the Winkler  $\text{O}_2$  method, used in all previous studies, because of its proneness to chemical interference. Also such before-and-after measurements assume a constancy of rate and thus an independence of the rate of oxygen consumption from the continually changing  $\text{O}_2$  tension. Values for respiration have been related to such parameters as the amount of chlorophyll, and thus, whatever their other usefulness, are awkward to employ on an area basis for ecological considerations.

It is now possible to monitor  $\text{O}_2$  tension continuously with an electrode (Kawisher, 1959). This is a physical method immune to chemical interference. We thought it worthwhile to make determinations of productivity of isolated corals using the oxygen electrode in a closed container *in vitro*, with carefully collected

corals under measured light intensities, to gain a more accurate notion of photosynthesis in individual coral heads.

## METHODS

### *A. Oxygen measurement*

A polarographic oxygen electrode inserted in a chamber with the coral sample continuously monitors the oxygen content of the sea water. Exchange at the free air surface was eliminated by a stopper. A short tube fitting over the electrode contained a stirring magnet supported on a shaft. This was rotated magnetically from outside. It kept the water at the electrode face well stirred (Kanwisher, 1959) and slowly mixed the contents of the chamber without agitating the coral polyps.

The temperature in the experimental chamber ranged from 28 to 31° C. The oxygen exchange at each light intensity was recorded for at least one hour. The electrode current was indicated on a potentiometer recorder from the voltage drop it produced across a thermistor molded in the electrode. The slope of the resulting temperature-compensated oxygen-time curve, combined with the amount of water in the chamber and the solubility coefficient of oxygen, allows the net exchange of the given coral specimen to be computed (Kanwisher, 1966). We then normalize this for the projected area normal to the light beam. Such a figure is equivalent to a rate per unit area of the bottom covered, the most direct way of expressing photosynthesis on the reef. One CO<sub>2</sub> molecule was assumed to be fixed for every O<sub>2</sub> molecule photosynthetically released. The productivity was then calculated as the rate of carbon fixation on an area basis.

The coral in the wide-mouth glass jar was illuminated by varying intensities from incandescent flood lights placed at different distances. The intensities were measured by a waterproof sensor held at the position of the coral surface. A water bath in the light path prevented temperature rise at high light intensities. A sample record is shown in Figure 1. The time constant of the electrode was 15 seconds for 90% response and the mixing time of the chamber was about 30 seconds. This method has been used extensively on sea weeds (Kanwisher, 1966).

Following such measurements on the coral species listed above, another set of measurements was made for a colony of *Dichococnia stokesii*. The coral tissue was then removed from the colony with a toothbrush and blasts of sea water until inspection with a stereomicroscope revealed no remaining tissue or zooxanthellae. This "cleaned" skeleton with its included boring algae was then reintroduced to the chamber and oxygen measurements were taken in dark and various light regimes.

### *B. Light measurements*

Light was measured for each experimental set-up with a logarithmic light meter calibrated to read footcandles of normal daylight spectral composition. The sensor consists of a network of photoresistive cadmium sulfide cells and fixed resistances such that the over-all resistance changed logarithmically with incident light intensity. A series battery and meter gives a reading proportional to resistance. The wavelength sensitivity curve of the cell plus an overlying filter restricts response to

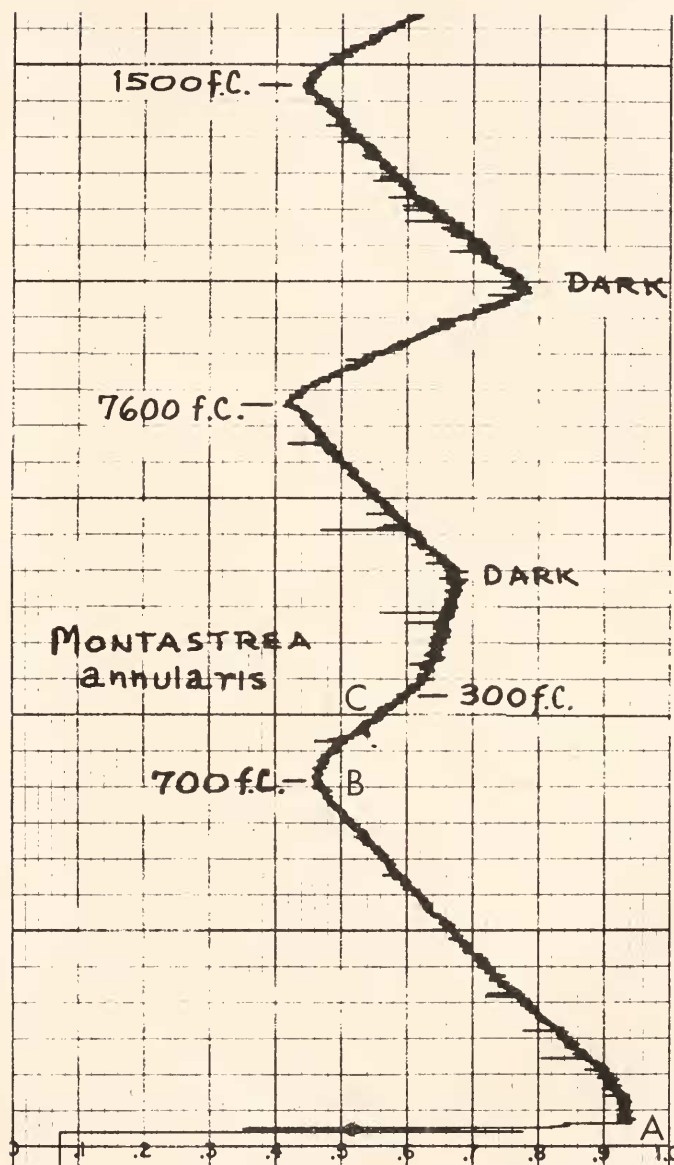


FIGURE 1. Sample chart record showing the time changes in oxygen produced by respiration and photosynthesis of the coral *Montastrea annularis*. Oxygen content of the sea water increases from 0 on the left to 4.5 ml./liter on the right. From A to B the coral is in the dark and the decrease in oxygen represents respiration. At B the coral is illuminated with 700 footcandles. The resulting photosynthesis is more than twice the dark respiration. For compensation this specimen requires less than the 300 footcandles applied at C. One hour equals 4 units.

wavelengths of 530 to 560 m $\mu$ . Since this is in the region of maximum transmission through sea water, the subsurface measurements probably indicate somewhat more total light over the whole visible range than there really is. Light is received over nearly a hemisphere. The same type of meter was used to measure light intensities inside living coral heads under water and through slices of clean coral skeleton under water in the lab.

A  $\frac{1}{2}$ " masonry bit in an electric hand-drill was used to bore holes into massive heads of *Montastrea annularis* from the back and from the side. The light sensor (cylindrical: 4 cm. long, 1.2 cm. diameter) could then be inserted into the hole. Light readings were taken in this manner in clean sea water. Corals were kept alive throughout this procedure: drilling was done while the tissues were immersed in sea water. These corals were handled and exposed to air briefly and no expansion of polyps was noted following drilling. Great care was taken not to touch the area of living tissue within 10 cm. of the point directly above the light sensor.

Slices of clean skeleton on *M. annularis* free of macroscopic associated boring organisms were cut 1 cm. thick with a hack saw using new blades that had been cleaned of paint. Cutting was done under flowing water, and packing of dust from the operation into the porous skeleton was thus avoided: sections were found to be clean by inspection with a stereomicroscope. Sections were cut tangentially and radially to the colony, perpendicular and parallel to axes of the calices, respectively. After cleaning the slices, light transmission was measured. The light sensor was held next to the coral slice and stray light from the sensor side was blocked by black cloth.

### *C. Boring algae*

Slices, and dissected bits of skeleton, of *Dichocoenia stokesii*, *Montastrea annularis* and *Mussa angulosa* were examined with a stereomicroscope. Bits of skeleton fixed in 10% neutral formalin in sea water were decalcified under observation in sea water in deep depression slides by adding 3% HCl a drop at a time. The organic remnants were observed up to 1000 $\times$  magnification using oil immersion objectives (n.a. 1.3). Thin sections of fixed, dried skeletons were cut and polished to uniform thickness. These were examined with direct microscopy under favorable conditions for the counting and measurement of algal filaments per unit volume of skeleton.

The distribution of boring algae was studied in *Montastrea annularis* by collecting numerous colonies of 10 to 40 cm. diameter, cracking them open along various planes, and observing and photographing the bands of green color. Bits of skeleton from the various green bands were fixed and studied microscopically to determine the state of the algal filaments. Pigment analyses were made on similar material.

## RESULTS

### *A. Respirometry*

Table I shows maximum figures for gross photosynthesis in grams of fixed carbon per square meter surface area of the bottom per 12-hour day and the



TABLE I

Calculated values of gross photosynthesis per unit surface area, maximum observed ratios of photosynthesis/respiration, and observed or estimated photosynthetic compensation light intensities for some Florida reef corals

Species	Gross photosynthesis q. C/m <sup>2</sup> /day	Maximum photosynthesis respiration	Compensation light intensity in footcandles
Gorgonacea			
<i>Plexaura flexuosa</i>	6.5	5.8	400
<i>Gorgonia ventalina</i>	6.8	3.0	300
<i>Briareum asbestinum</i>	3.7	2.5	400
<i>Erythropodium caribaeorum</i>	5.8	4.2	600
Scleractinia			
<i>Siderastrea siderea</i>	4.0	2.1	300
<i>Porites divaricata</i>	10.2	3.4	600
<i>Favia fragum</i>	4.2	2.3	400
<i>Manicina areolata</i>	5.2	2.4	—
<i>Montastrea annularis</i>	9.5	2.9	200
<i>Oculina diffusa</i>	8.4	5.0	—
<i>Dichocoenia stokesii</i>	8.0	—	300
<i>Mussa angulosa</i>	2.7	1.9	300
<i>Isophyllia multiflora</i>	7.9	5.0	400
<i>Colpophyllia</i> sp.	5.4	3.2	700

maximum photosynthesis-to-respiration ratio for each species. Also given is the observed or estimated light intensity in footcandles for photosynthetic compensation. Attention is called to the fact that these figures are not true measures of the performance of algae, but they represent the total respiratory and photosynthetic balance of coral tissue plus zooxanthellae plus other organisms inhabiting the skeleton. Figure 1 shows a typical respirometer record. For any given part of the trace between changes in light intensity, the slope was calculated for the last part of the time in that light regime.

Oxygen production of the boring algae in the "cleaned" skeletons of *Dichocoenia* could not be detected. Oxygen consumption in the dark was measured on both colonies that were treated in this way, but no change in slope of the respirometer trace was detectable following the onset of light intensities of 400 and 5000 footcandles for 1.5 hours.

In our fervor to have polyps expanded we nearly missed seeing the striking effect polyp contraction has in gorgonians. Jarring the respirometer caused *Erythropodium* to contract its polyps during the experiment and external evidence of respiratory exchange all but vanished. We were unable to discern which of two probable causes may have been most important in this apparent inhibition: (1) There is a considerable in- and out-going circulation of sea water created by cilia in the vast system of gastrodermal canals deep inside the colony. When mouths are open this mixing would carry results of gaseous exchange outside the colony very rapidly. When polyps are contracted within the colony, gaseous exchange must be *via* diffusion through the rather dense tissues and would thus be greatly retarded. (2) Mesodermal spicules of calcite are highly refractive to

TABLE II

*Light intensity values in footcandles at various depths on the reef*

Cloud conditions	Depth m.	Light intensities in footcandles
Bright sun 9:45-11:30 AM over sand	0	4500
	8 on bottom	1000
	0	4500
	4 on bottom	1000
	0	4500
	30 on bottom	400
Nearly complete cloud cover over sand	0	2000
	5 on bottom	1000
	0	2000
	4 on bottom	100

light and often highly pigmented. It is possible that algae in contracted polyps are shielded from light and thus photosynthesis is retarded or prevented.

*B. Light intensities* (see Table II).

*C. Boring algae*

The only genus of alga observed in skeletons of living coral in this study is *Ostreobium* (Bornet and Flahault, 1889), a siphonaceous green alga. In massive corals such as the dominant Caribbean reef-builder *Montastrea annularis* there are alternating green and white layers arranged concentrically around the point of first growth. These layers are seen as dark bands in the split coral head shown in Figure 2. Each green band is formed at the growing surface of the coral and although the algal filaments are inside the aragonite of the skeleton, they extend to the very surface of the skeleton and thus lie within 0.1 mm. of the skeletogenic tissues of the coral. It is possible that they contact coral tissue. Algal filaments can be isolated from any of the green bands in a coral head. In healthy living heads with few associated boring organisms, only *Ostreobium* was found.

However, in the microscopic examination of fixed material, the green bands found within 1 cm. of the surface of the colony were the only green bands containing algal filaments with recognizable chloroplasts and whose entire cytoplasm had the appearance of one which had been fixed while alive. Only the very outside green band had a preponderance of algal filaments that appeared, by such criteria, to be living. In deeper green bands a larger proportion of the green pigment was seen to be in the mineral of the skeleton. It presumably had diffused out of the filaments and had been adsorbed by the aragonite of the skeleton.

In one of the specimens of *D. stokesii*, whose skeleton and included algae were examined by respirometry, counts of algal filaments were made per unit volume of solid skeleton. Since filaments of *Ostreobium* have no cross-walls, cell counts could not be made. However, in solid skeleton where there is relative homogeneity of

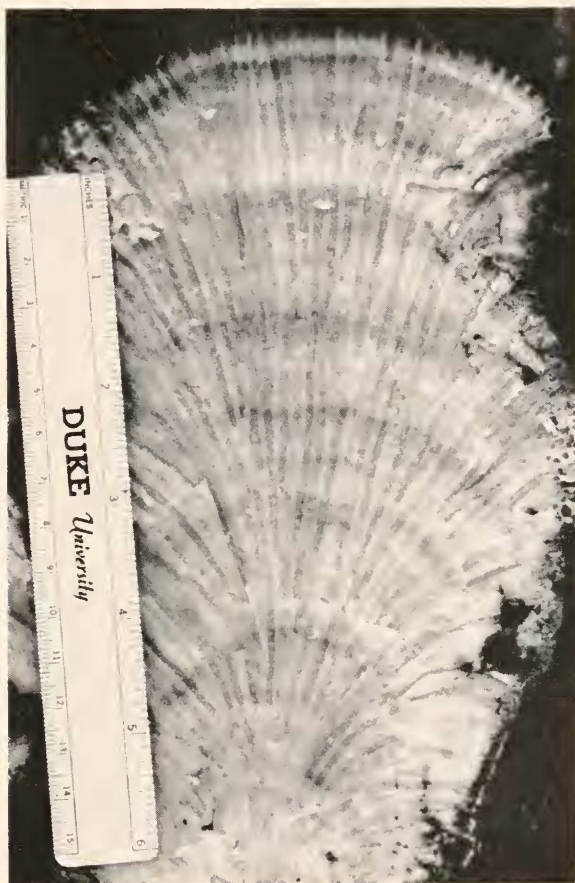


FIGURE 2. Internal (broken) surface of a head of the stony coral, *Montastrea annularis*, that has been split vertically. Concentric dark bands are the green bands referred to in the text. Vertical lines are now empty calices of individual polyps. The living coral tissue occupies the topmost layer of ca. 3 mm. thickness.

structure over volumes as large as a few  $\text{mm}^3$ , the algal filaments grow more or less straight and parallel to each other. In any particular field of view, the number of forks is roughly equal to the number of filament terminations. Filaments are assumed to be straight and perfectly cylindrical in the calculations. Since neither is precisely the case, the estimate of volume of algal filaments is lower than the actual value. By count in volumes of the order of  $0.01 \text{ mm}^3$  in the darkest green zone, there are approximately 1500 algal filaments per  $\text{mm}^3$ . At an average diameter of  $10 \mu$  per filament, the skeleton would contain 12% by volume of algae.

#### D. Pigments

The layer of coral polyps with its contained zooxanthellae forms a continuous sheet over the surface of the colony. The photosynthetic pigments of these algae



TABLE III

*Light penetration into whole heads and clean skeleton of Montastrea annularis*

Specimen	Depth of sensor in head in mm, from lighted surface	Light intensity at surface of coral in footcandles	% Light transmitted
Head # 1	16	6600	0.20
Head # 2	10	4500	0.78
Head # 3	10	5200	0.15
Head # 4	5	6500	0.92
Head # 5	4	3000	1.00
Tangential slice from top of head	5 mm. thick	450	1.9
Tangential slice of clean skeleton	10 mm. thick	3000	3.0
Radial slice of clean skeleton	10 mm. thick	3500	2.8

color the coral olive green to brown. A species such as *Montastrea annularis* may be a dark chocolate brown in color. The same species will appear nearly colorless without the zooxanthellae. The underlying chlorophyll of the boring green filaments rarely shows by inspection from the outside. Some corals, such as species of *Porites*, have smaller amounts of brown animal pigments.

A square column extending from the surface down into the coral head was cut with a glass-cutting saw. The successive colored layers were then sliced off, ground and extracted, and absorption spectra obtained with a spectrophotometer. The 2-mm. surface layer contained all the coral polyps and thus all the zooxanthellae plus a small amount of boring green algae. All succeeding layers below had only green filaments.

The absorption curve of the surface layer showed mostly accessory pigment (carotenoids) bands with the chlorophyll only scarcely visible. We estimate that a minimum of 80% of incident light is absorbed by accessory pigments. It seems unreasonable to give the zooxanthellae a less important role in the total oxygen exchange of a coral head than the subsurface green filaments only because they have less extractable chlorophyll (Odum and Odum, 1955).

Extracts of the green bands in the skeleton below the polyp layer (Fig. 2) showed only chlorophyll-type absorption peaks. Chlorophyll and its degradation product phaeophytin were determined after the method of Yentsch and Menzel (1963). A large part of the green coloring—particularly below the topmost band—was due to phaeophytin, the magnesium-free form of chlorophyll. This fraction cannot be active photosynthetically. Three things (1) the fact that only boring algae of the outermost layer appear to be intact, (2) the photosynthetically inactive nature of the subsurface layers combined with the very low light levels beneath the outer layer, and (3) our inability to measure photosynthesis when the coral tissue was removed, make it difficult for us to conclude that boring algae are major producers in coral heads from Florida reefs.

#### DISCUSSION OF EXPERIMENTS

The respirometric data here concern coral colonies in confined spaces for short-term experiments. Thus discussion preceding conclusions will be related to this situation only. The work was done out of interest in the ecology of corals and

their associated algae. We will put forth our own suggestions and hypotheses on these matters following conclusions drawn from the data.

Some approximations are necessary for the calculations whose results appear in Table I. The respiratory consumption of oxygen in some species is markedly dependent on oxygen tension. We chose the value at air saturation since this is the range where the coral must operate in nature. The estimate of area for some of the branching species may be as much as 25% in error.

Several facts are clear from the oxygen-time curves such as Figure 1 and the resulting data in Table I. All coral species were able to photosynthesize more than the respiratory needs of the entire head. In all but one, *Mussa*, this gross productivity was more than twice as great, so that 12 hours of usable light would more than make up for the 24-hour respiratory need. Compensation intensity was usually 300–500 footcandles, much less than the average illumination level (Table II). Thus most shallow-water corals should be photosynthesizing more than all their respiratory needs.

Any artifact of handling or making a measurement in a closed chamber should reduce the rate of photosynthesis. Thus the productivity measurements given here are a minimum. In spite of this, the lowest productivity we record from a coral head is higher than that for any planktonic situation in the open sea. The highest, at 10 g. C/m.<sup>2</sup>/day, is within a factor of 2 of Ryther's (1959) estimate of the theoretical maximum based on quantum efficiency and available sunlight. Such high values of productivity indicate that most of the light incident on a coral is absorbed by photosynthetic pigment. At illumination levels around compensation the computed photosynthetic efficiencies were about 10%, which is also close to the theoretical maximum.

The light reaching the boring filamentous algae in the coral skeleton is low, about 1–2% of that incident on the outer coral surface. The latter in clear weather may be 2500 to 5000 footcandles. Thus the upper filamentous green layer would have only 25 to 50 footcandles available. If it used all of this with the expected quantum efficiency the resulting carbon fixation could only be 0.2 to 0.4 g. C/m.<sup>2</sup>/day, a small part of the observed for whole coral heads. It is irrelevant to consider whether the algae have a low compensation intensity since the net production can never be larger than this. From this and the fact that gorgonian corals contain no filamentous algae and still show high photosynthetic rates, we conclude that skeleton-boring algae are responsible for less than 10% of the total primary productivity of a coral head.

Except for Beyers (1966) and Roffman (1966), all previous workers have reported gas exchange in corals per unit nitrogen or chlorophyll or weight of coral. Since these parameters vary significantly among species and even within a single coral head, results based on them are not comparable and are difficult to interpret at all. We believe the only basis for comparison is the projected surface area of the colony that receives light. Since sunlight shows little directionality in the habitats of the corals we chose for experimentation, total surface area of living tissue was estimated.

#### GENERAL DISCUSSION

We are concerned here with how much photosynthesis occurs on a coral reef in nature, which of the associated plants is responsible for this, and how it potentially

may influence the coral. By primary productivity we mean the rate of carbon fixed per area of the reef. We have used the usual units of grams of carbon  $\times$  meter<sup>-2</sup>  $\times$  day<sup>-1</sup>. In any square meter of reef surface there can be many square meters of coral surface. In an area of crowded branching corals, the potentially high productivity is not realized because of mutual shading. The analogous case of a dense sea weed stand has recently been worked out by Kanwisher (1966).

When oxygen production was measured at several light levels, the resulting curve showed a linear increase with intensity up to saturation (usually about 2000 footcandles) and then little further increase beyond this. As in sea weeds (Kanwisher, 1966) there was no sign of photosynthetic inhibition at values approaching full sunshine.

Full sunshine gives a theoretical maximum of about 100 g. C/m.<sup>2</sup>/day. The intensity at which saturation occurs is about  $\frac{1}{3}$  of sunshine. This immediately reduces the production to 20 g. C/m.<sup>2</sup>/day since all excess quanta are wasted. As shown with sea weeds the potential photosynthesis per unit area may be many times this. But it cannot be realized because there is not a dense enough flux of light any place in nature. Thus it is ecologically invalid to relate photosynthesis to the amount of pigment, the weight of tissue, etc., since the mere capacity for photosynthesis does not guarantee that it will be used. In spite of Beyers' findings (1963, 1966) and warning (1965, p. 73) concerning the variation in photosynthetic rates of organisms over normal days, our experiments have all been of short duration. Roffman (personal communication) finds the same decrease in photosynthetic rate in both Caribbean and Pacific corals in short-term experiments. We offer no explanation for this phenomenon nor for our failure to observe it.

The filamentous green algae seem unlikely as a major source of photosynthetic gas exchange because of the long diffusion path to the outside. Both time and rate play a part in our formulation of such a conjecture. When the light intensity on a coral was changed, the oxygen curve reached its new slope in 3 to 5 minutes. This includes time for mixing in the chamber and the response time of the electrode, as well as the establishment of the new diffusion gradient within the coral. From the known diffusivity of dissolved oxygen, it follows that the distance from the major source of photosynthesis to the sea water outside is less than 1 mm. If we consider a layer 1 cm. below the surface, it would take 12 hours to reach 95% of its equilibrium gradient. In addition, the resulting flux of oxygen outward would be less than 1% of what we measured, even with a  $pO_2$  of 1 atmosphere in the algal layer. If the deeper green layers were contributing importantly in the oxygen flux, it would be necessary to use something analogous to the extensive capillary vascular system of higher animals where mass transfer rather than diffusion is the dominant process. The volume of water in the algal channels represents too small a reservoir of nutrients and  $CO_2$  for more than a few minutes of rapid photosynthesis. For these reasons we feel that the underlying green algae are too isolated to be contributing a major component of the gas exchange we are observing. There is always danger in extrapolating from results of experiments on Caribbean corals to the situation in the tropical Pacific Ocean. Since no worker has published comparisons of corals or their included algae from the two regions, one cannot estimate the error involved in extrapolations from our results to Pacific corals. Since our experimental corals were taken from depths of 5 to 9 m., they are perhaps still less comparable to the Pacific corals that have given rise to speculation on

these matters. Total pigmentation and even morphology of coral polyps varies considerably from the top of a large massive head of *Porites*, for example, that may be just sublittoral, to the sides and bottom of the same head 2 m. further from the sea surface. It is possible that in very shallow water the pigmentation of corals and their algal components may be balanced in such a way that the latter are the chief primary producers. We would like to see both physiological data and pigment analyses to test this hypothesis.

Although the green algae appear to contribute at best only a minor part to coral productivity, it is interesting in terms of their own physiology that they are able to grow at all under such conditions of limited light and diffusion access to the outside. Since we are unable to detect any photosynthetic oxygen production by them, we cannot say what their compensating light intensity is. Sea weeds may have a value as low as 25 footcandles (Kanwisher, 1966). This is approximately the level of light penetrating the overlying polyp layer. Thus it is not impossible that the uppermost green layer can photosynthetically produce its respiratory needs and perhaps grow slowly. We would also like to point out the possibility of heterotrophic nutrition which is common among diatoms (Lewin, 1953). One of us (JWK) has frequently found filamentous green algae in dark anaerobic sediments where heterotrophic growth would seem the only explanation.

Oxygen measurements such as ours tell nothing about the eventual fate of the fixed carbon, but the possible alternatives can be inspected. First, the production may be used in the growth of the zooxanthellae. The excess cells produced, if any, can either be released to the outside or consumed by the coral itself. In either case there could be a rapid growth with a doubling of zooxanthellae numbers at least once a day (Kanwisher, 1966), and such rates are characteristic of single-celled plants. Only once in 30 hours' SCUBA diving, day and night, did we observe a coral, *Diploria strigosa*, extruding strings of brown slime that may have contained zooxanthellae. Goreau and Goreau (1960) and Muscatine (1967) have provided information that supports the notion that photosynthates are released by the zooxanthellae and are taken up by animal cells.

In summary, it seems to us that trophic interrelationships of corals and their included algae, both intracellular and skeletal-boring, are not yet fully understood. Experimental information thus far indicates that zooxanthellae can produce more than enough fixed carbon compounds to compensate for the carbon lost through respiration of the coral head. The excess, if it is real, must represent a net export from the coral reef, probably either as dissolved organic material or as detritus. One can be sure that the nutritional story of boring algae will be an interesting one, but we feel that the role they play in the primary productivity of the entire coral head will be found to be a minor one.

#### SUMMARY

Oxygen exchange is reported for 14 species of Florida reef corals in the dark and at different light intensities. Oxygen tension was monitored with a recording polarographic electrode. Results are given as grams of carbon fixed per square meter of coral surface per day, and compensation light intensities were given for each species. Maximum ratios of photosynthesis to respiration varied from 1.9 to 5.8. Boring, filamentous green algae living in the skeleton of *Dichocoenia stokesii*



were not observed to change their rate of oxygen consumption from dark conditions up to 5000 footcandles of light. It is concluded that reef corals are among the most productive organisms known and that, in Florida corals, the boring green algae contribute very little indeed to this productivity. Some data are given on the light impinging on Florida reefs and the light penetrating coral skeleton. Reasons for believing boring green algae are of minor importance are given in the discussion.

#### LITERATURE CITED

- BEYERS, R. J., 1963. A characteristic diurnal metabolic pattern in balanced microcosms. *Publ. Inst. Mar. Sci., Texas*, 9: 19-27.
- BEYERS, R. J., 1965. The pattern of photosynthesis and respiration in laboratory microecosystems. *Mém. Inst. Ital. Idrobiol.*, Suppl. 18: 61-74.
- BEYERS, R. J., 1966. Metabolic similarities between symbiotic coelenterates and aquatic ecosystems. *Arch. Hydrobiol.*, 62: 273-284.
- BORNET, E., AND C. FLAHAULT, 1889. Sur quelques plantes vivant dans le test calcaire des mollusques. *Bull. Soc. Bot. France*, 2e sér: CXLVII-CLXXVII.
- BURKHOLDER, P. R., AND L. M. BURKHOLDER, 1960. Photosynthesis in some alcyonacean corals. *Amer. J. Bot.*, 47: 866-872.
- FRANZISKET, L., 1964. Die Stoffwechselintensität der Riffkorallen und ihre ökologische, phylogenetische und soziologische Bedeutung. *Z. vergl. Physiol.*, 49: 91-113.
- GOREAU, T. F., AND N. I. GOREAU, 1960. Distribution of labelled carbon in reef-building corals with and without zooxanthellae. *Science*, 131: 668-669.
- KANWISHER, J. W., 1959. Polarographic oxygen electrode. *Limnol. and Oceanog.*, 4: 210-217.
- KANWISHER, J. W., 1966. Photosynthesis and respiration in some seaweeds. In: *Some Contemporary Studies in Marine Science*, H. Barnes, Ed., 407-420. George Allen and Unwin, London.
- KAWAGUTI, S., 1937. On the physiology of reef corals. I. On the oxygen exchange of reef corals. *Palao Trop. Biol. Sta. Stud.*, 1: 187-198.
- LEWIN, J. C., 1953. Heterotrophy in diatoms. *J. Gen. Microbiol.*, 9: 305-313.
- MUSCATINE, L., 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. *Science*, 156: 516-519.
- ODUM, H. T., AND E. P. ODUM, 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.*, 25: 291-320.
- RYTHER, J. H., 1959. Potential productivity of the sea. *Science*, 130: 602-608.
- YENTSCH, C. S., AND D. W. MENZEL, 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Res.*, 10: 221-231.
- YONGE, C. M., M. J. YONGE AND A. G. NICHOLLS, 1932. The relationship between respiration in corals and the production of oxygen by their zooxanthellae. *Sci. Rep. Gr. Barrier Reef Exped.*, 1: 213-251.